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ARE RESULTS OF ARTIFICIAL NEST EXPERIMENTS A VALID INDICATOR OF SUCCESS OF NATURAL NESTS?

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ABSTRACT.—Studies using artificial nests to assess rates or patterns of nest predation have increased during recent decades. However, the critical assumption that temporal or spatial patterns of relative predation rates of artificial nests parallel those of natural nests has begun to be questioned. We compared the daily survival rate for 365 artificial nests with that estimated for 295 open nests of passerines, and analyzed the trends in survival rates for both nest types among three breeding seasons and three species of nest plants in the central Monte Desert, Argentina. Daily survival rate for artificial nests (0.737) was significantly lower than that for natural nests (0.925). Trends in survival rates of artificial nests over years and among species of nest plants only partially reflected those of natural nests. Our results support the well established finding that artificial nests may not accurately estimate actual rates of nest predation. Artificial nests may provide an additional source of data to natural nests when testing ecological hypotheses, but artificial nest experiments should be carefully designed (i.e., realistic) and should attempt to identify predators of artificial and natural nests to validate the experimental results. *Received 24 October 2002, accepted 10 March 2003.*

The main cause of nest mortality in most bird species is predation (Ricklefs 1969, Rotenberry and Wiens 1989, Martin 1993, Mezquida and Marone 2001). However, it often is difficult to obtain the appropriate number of natural nests to assess different factors influencing rates of nest predation (Reitsma et al. 1990). For this reason, the use of artificial nests to estimate nest predation rate has increased during the last few decades (reviewed in Major and Kendal 1996, Sieving and Willson 1998, Schmidt and Whelan 1999). Major and Kendal (1996) summarized the diverse, and sometimes nonrigorous, field techniques used in these types of experiments that at times make analysis of pattern consistency difficult.

Absolute rates of predation on artificial nests commonly have been found to differ from those of natural nests. Some authors have found similar predation rates in artificial and natural nests (see references in Major and Kendal 1996), but most studies have shown either lower predation pressure for natural compared to artificial nests (Bechet et al. 1998, Sloan et al. 1998, Wilson et al. 1998, Zanette 2002) or more intense predation on natural nests (Chamberlain et al. 1995, Davison and Bollinger 2000). However, this is not necessarily a problem for comparative studies on artificial nests. Despite the fact that absolute predation rates may differ between natural and artificial nests, inferences derived from artificial nests can be valid if relative predation rates follow a similar and consistent trend in both types of nests. This assertion, commonly used to justify the artificial approach, usually has not been tested and the results at hand are conflicting. In some studies, rates of predation for both nest types did not follow the same pattern (Willebrand and Marcstrom 1988, MacIvor et al. 1990, Buler and Hamilton 2000), while trends were similar for artificial and natural nests in other studies (George 1987, Ammon and Stacey 1997, Wilson et al. 1998). Moreover, when a series of treatments was considered in the study (e.g., types of artificial nests, spatial and temporal variations), the relationship between the success of artificial and real nests usually differed among subsets of data (Butler and Rotella 1998, Davison and Bollinger 2000, Weidinger 2001a, Zanette 2002).

In this study, we examined whether predation on artificial nests reflects that of natural nests of passerines in an area of southern South America. We compare absolute rates of predation of artificial and natural nests. We also compare trends in predation rates for ar-

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TABLE 1. Nests of 15 species of open-nesting passerines from Ñacuñán made up the sample of natural nests used for survival rate calculations.

Species	Number of nests
Ringed Warbling-Finch, *Poospiza torquata*	95
Gray-crowned Tyrannulet, *Serpophaga griseiceps*	74
Cinnamon Warbling-Finch, *Poospiza ornata*	53
Greater Wagtail-Tyrant, *Stigmatura budytoides*	18
Many-colored Chaco-Finch, *Saltatricula multicolor*	16
Crowned Slaty-Flycatcher, *Empidonomus aurantioatrocristatus*	12
White-banded Mockingbird, *Mimus triurus*	11
Black-crowned Monjita, *Xolmis coronata*	4
Scrub Flycatcher, *Sublegatus modestus*	4
Golden-billed Saltator, *Saltator aurantiirostris*	2
Yellow-billed Tit-Tyrant, *Anairetes flavirostris*	2
Fork-tailed Flycatcher, *Tyrannus savana*	1
Rufous-collared Sparrow, *Zonotrichia capensis*	1
Vermilion Flycatcher, *Pyrocephalus rubinus*	1
White-tipped Plantcutter, *Phytotoma rutila*	1
Total	295

tificial and natural nests both temporally (across three breeding seasons) and spatially (across three species of nest plants), and discuss the validity of using trends observed in artificial nests to infer trends in natural nests.

METHODS

We conducted this study in the Biosphere Reserve of Ñacuñan (34° 03′ S, 67° 54′ W), Mendoza province, Argentina. The reserve is located in an alluvial plain of the central Monte Desert and comprises an open *algarrobo* (*Prosopis flexuosa*) woodland with scattered chañar trees (*Geoffroea decorticans*), abundant tall shrubs >1 m tall (*Larrea divaricata*, *Capparis atamisquea*, *Atriplex lampa*), low shrubs <1 m tall (mainly *Lycium* spp.), and perennial grasses (*Pappophorum* spp., *Trichloris crinita*, *Setaria leucopila*, *Digitaria californica*, *Aristida mendocina*). Annual forb cover is highly variable from year to year and usually lower than grass cover. The climate of Ñacuñan is dry and temperate, with cold winters. Most precipitation (78% of annual rainfall) occurs during the spring and summer months (October to March; Marone et al. 2000).

Birds such as the Chimango Caracara (*Milvago chimango*) and Brown Cacholote (*Pseudoseisura lophotes*) appear to be the most important nest predators in the reserve, although some mammals such as the small fat-tailed opossum (*Thylamys pusilla*, Didelphidae) and the little grison (*Galictis cuja*, Mustelidae) also have been confirmed as nest predators (Mezquida and Marone 2002). Other potential predators include the white-eared opossum (*Didelphis albiventris*, Didelphidae), Molina's hog-nosed skunk (*Conepatus chinga*, Mustelidae), South American grey fox (*Dusicyon griseus*, Canidae), and small snakes.

Natural nests.—During spring and summer (October to March) from 1996–1997 to 1998–1999 (i.e., three breeding seasons), we located open nests of passerines by systematic searches in the vegetation and by following adult birds (Martin and Geupel 1993). Most nests were placed in chañar and zampa (*Atriplex lampa*), two plant species widely used for nesting in this area (Mezquida and Marone 2001). All nests included in our sample of natural nests (see Table 1) were found in the shrub-midstory (≤1.5 m) or canopy-subcanopy (>1.5 m) strata. Nests placed in these two strata showed similar survival rates (Mezquida 2000). Each nest was visited every 1–3 days until it either failed or fledged young. Nests that fledged at least one young were considered successful. A nest was considered depredated when all the eggs or young nestlings disappeared (see Mezquida and Marone 2001 for further details).

Artificial nests.—Concurrent with our studies of natural nests, we conducted artificial nest experiments. In the open woodland habitat, we established two or three divergent transects (≥200 m apart at origin) along scarcely used tracks inside the reserve. On each transect, we tied small pieces of colored tape to vegetation, alternating on the right and left side of the track, at 40–50 m intervals. One nest was placed more than 20 m from each mark in a perpendicular direction to the transect. To aid in locating nests again, we tied a new mark to the vegetation, in most (>80%) cases >10 m from the nest, following suggestions by Major and Kendal (1996). Artificial nests were open cup natural nests collected during the previous breeding season, mainly Ringed Warbling-Finch (*Poospiza torquata*) and Cinnamon Warbling-Finch (*P. ornata*) nests. All of the nests we used in the experiments were small cups made of grasses with an external diameter of 6–7 cm and an external height of 5–6 cm. We placed the nests in three plant species, chañar, jarilla (*Larrea* spp.), and zampa, trying to imitate natural positions. Range of nest heights in each plant were 1–2 m (chañar), 0.5–1.0 m (jarilla), and 0.5–1.0 m (zampa). Each nest was baited with two fresh quail (*Coturnix* sp.) eggs. Quail eggs are bigger than those of the local passerines. However, the use of these eggs in our experiments does not appear to have biased our results (see Discussion). Total exposure period was 12 days for each experiment, similar to the mean incubation period of the passerine assembly breeding in the area (Mezquida and Marone 2001). We checked the nests every two days taking care to approach the nests from different directions to avoid creating obvious paths for potential predators. When we detected the presence of a potential predator, we did not approach the nest until the predator moved away. Artificial nests with both eggs missing or damaged were classified as depredated. Therefore, nests with one or both eggs undamaged at the end of the experiment were considered successful. Artificial nests and eggs were removed when the nest was considered depredated or after the exposure interval if survival occurred.

Analyses.—We calculated the daily survival rate of natural and artificial nests using the Mayfield method (Mayfield 1975), and its associated variance (Johnson 1979). For natural nests, we included only nest mortality caused by predation and using this, we calculated daily predation rate (m_p). Daily survival rate to predation (s_p) was equal to $1 - m_p$. We estimated total exposure days as the interval between the day when the nest was found active (i.e., with eggs or nestlings) and the fledging of the young or halfway between the two subsequent visits between which a nest failed. We counted total exposure days for artificial nests in a similar way. Nest mortality (mainly due to predation) for natural nests was very high during our study (usually <80%; Mezquida and Marone 2001). Therefore, to increase sample size and the confidence of survival rate estimates, we calculated the daily survival rate of natural nests during the egg and nestling period as a whole, because daily survival rates did not differ significantly between the two stages (Mezquida and Marone 2001). We used the Hensler and Nichols (1981) test to test for differences in daily survival rate between artificial and natural nests. We compared daily survival rates for artificial and natural nests among years and nest plants using methods described by Aebischer (1999). We tested the goodness-of-fit of different models for each two-way comparison (i.e., nest type × year and nest type × nest plant) and used likelihood-ratio tests for comparisons between models.

RESULTS

We distributed 365 artificial nests in the open woodland, 353 of which were depredated during 1,344 exposure days. The sample of natural nests included 295 nests of 15 bird species, although most (95%) nests were of the seven most numerous species (with more than 10 nests each; Table 1). During a total of 2,628.5 exposure days, 197 natural nests failed due to predation. The resulting daily survival rates were significantly lower for artificial nests (daily survival probability ± associated variance = $0.737 \pm 1.4 \times 10^{-4}$) than for natural nests ($0.925 \pm 2.6 \times 10^{-5}$; Hensler and Nichols test, $Z = 14.4$, $P < 0.0001$).

The full model that included the main effects of nest type, year, and the interaction between them (deviance = 567.5, df = 654, $P = 0.99$) fitted well. The comparison of the full model with a model with main effects only (deviance = 1378.3, df = 656) showed that there was a significant interaction between

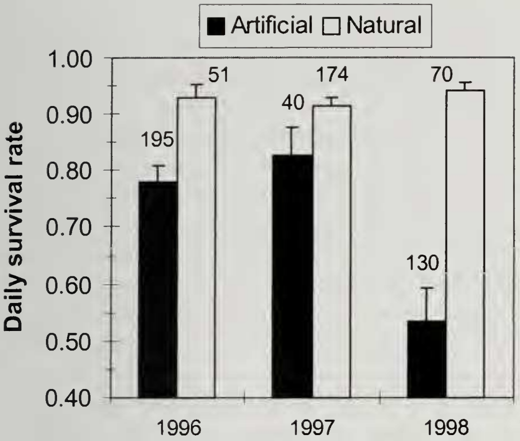

FIG. 1. Daily survival rates of artificial nests were always lower than those of natural nests during the three years studied, but was especially low for artificial nests during 1998. Daily survival rates, 95% confidence ranges (Hensler and Nichols 1981) and number of nests are shown for artificial and natural nests during three breeding seasons (austral spring and summer) in the Reserve of Ñacuñan, Argentina.

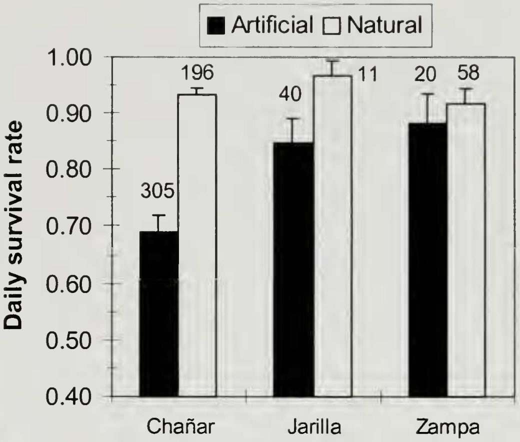

FIG. 2. Daily survival rates of artificial nests were consistently lower than those of natural nests in all nest plants, but the relative rate for artificial nests placed in zampa was higher than that of natural nests. Thus, both nests types showed nonparallel trends. Bars represent the daily survival rate and the 95% confidence range of each nest type in three plant species at Ñacuñan, Argentina. Sample sizes are indicated for each group.

nest type and year (D = 810.8, df = 2, $P < 0.0001$). A model that included the main effect of nest type (deviance = 610.0, df = 658, $P = 0.91$) showed a good fit, whereas a model with just temporal effects was rejected (deviance = 768.2, df = 657, $P = 0.002$). Thus, the daily survival rate of artificial nests was consistently lower compared to natural nests, but was particularly low during 1998, causing an interaction between nest type and year (Fig. 1).

Similarly, a full two-way model with interactions to examine the effect of nest type and species of nest plant on daily survival rates showed a satisfactory fit (deviance = 535.6, df = 624, $P = 1.00$). The likelihood-ratio test that compared the full model with a two-way model without interactions (deviance = 1306.9, df = 626) was significant (D = 771.4, df = 2, $P < 0.0001$), indicating a significant nest type × nest plant interaction. A model specifying just nest type effects (deviance = 569.5, df = 628, $P = 0.95$) showed a good fit, whereas a model with just nest plant effects (737.4, df = 627, $P = 0.002$) fitted poorly. The daily survival rates were lower for artificial nests in all nest plants, but increased from chañar to zampa, whereas the daily survival rates of natural nests in chañar and zampa were lower than that in jarilla (Fig. 2).

DISCUSSION

Our results, in agreement with other findings, showed that artificial nests suffered higher predation pressure than natural nests (Sloan et al. 1998, Wilson et al. 1998, Zanette and Jenkins 2000). However, this is not surprising because most studies comparing absolute rates of predation between artificial and natural nests have found differences. Many factors might explain the discrepancy in the probability of every nest type being predated (reviewed in Major and Kendal 1996). Although studies designed for one or a small number of bird species could better simulate natural conditions, our artificial nests were reasonably realistic. We did not use artificial structures (e.g., wire baskets, tennis balls) to simulate nests, but natural nests in order to avoid artificial biases (Martin 1987). Further, we placed the nests in plants and positions based on previous knowledge of the nesting ecology of local passerines in the study area.

In contrast, the use of quail eggs in the artificial nests might justify some criticism suggesting that our predation rate estimates are biased. The size of quail eggs (mean length:

32.7 mm, $n = 60$) was larger than the mean egg size for bird species included in the sample of natural nests (19.9 mm, $n = 15$ species; Mezquida 2000), which could have increased the detectability of eggs in artificial nests. However, some small-mouthed nest predators are unable to break quail eggs (Roper 1992, Haskell 1995), and others do not appear to consume this type of egg (Marini and Melo 1998). Hence, the use of commercially available eggs might under- as well as overestimate predation rate on artificial nests. The results of specific experiments conducted at the Reserve of Ñacuñan suggested that this potential bias was a minor one; the predation rate for artificial nests baited with eggs that more accurately resembled eggs of the local passerine species was similar to the predation rate for nests baited with quail eggs (Quse 2001). The pattern of egg coloration also differed between quail and natural eggs, although previous studies indicate that egg color does not seem to affect predation rate (Jobin and Picman 1997, Weidinger 2001b).

Even though results of experiments using artificial nests do not generally offer realistic indicators of actual nest predation, this might not invalidate their use if patterns or trends (i.e., relative rates of predation) among treatments are similar in both nature and experiments. However, studies comparing the success of artificial and natural nests in different treatments (e.g., habitats, patches, years) have obtained conflicting results, as in the present study. Our results show that patterns of predation of artificial nests across years and species of nest plants did not closely parallel those found for natural nests. In our first comparison, the survival rate of artificial nests during the first two breeding seasons followed the same trend as in natural nests, but the pattern differed during the next breeding season. The decreased survival rate of artificial nests over time might be a consequence of predators learning to find artificial eggs (Major and Kendal 1996, Vander Haegen and DeGraaf 1996). For example, Buler and Hamilton (2000) also observed an increase in predation of artificial nests between two consecutive years, contrary to predation of natural nests, and suggested the potential for learning by predators (mainly crows). In Ñacuñan, we did not use the same transects for later trials, but we used the same general area to place artificial nests in successive years, probably facilitating predators to learn to detect our proffered nests.

Another comparison showed that the survival rate of artificial and natural nests differed depending upon the species of plant that supported the nest, but patterns were not fully similar for both nest types. The survival rate of artificial nests was lowest in chañar and highest in zampa. Chañares are small trees with small and dispersed leaves, while zampas are medium-sized and compact shrubs with abundant evergreen leaves. Thus, the pattern of predation on artificial nests suggests that the degree of nest concealment might have played a role. Moreover, birds appear to be major nest predators at our study area (Mezquida and Marone 2002), and these visual predators probably were very efficient at detecting our artificial nests, mainly those placed in chañar that were higher and less concealed. Other studies also have suggested that the degree of concealment is an important factor that affects success of nests unattended by parents (Götmark et al. 1995, Major and Kendal 1996, Cresswell 1997). Natural nests also suffered high predation pressure, but rates for nests built in chañar and zampa were similar. In contrast to artificial nests, the relative incidence of terrestrial predators (i.e., mammals and reptiles) on natural nests in zampa presumably would be higher, due to the presence of parents and the activity at the nests (Davison and Bollinger 2000).

In conclusion, our results for a location of central-western Argentina add new evidence to the well established pattern that artificial nests are not always a trustworthy indicator of predation rates on natural nests. Whether absolute rates of predation on artificial nests are higher or lower than those on natural nests probably depends upon characteristics of the artificial setup (e.g., nest site and position, nest type) and the kind of predators involved. Our study also showed that temporal and spatial trends in daily survival rates of artificial nests did not closely correspond with those of natural nests. Differences suggest behavioral responses by predators and that, at least in some situations, both types of nests may not attract the same predators. We recommend that future studies using artificial nests should be realistic (i.e., based on the nesting ecology of the target species) and concurrent with a study on natural nests, and should attempt to identify predators of both nest types to validate the experimental results. In addition to natural nest experiments, carefully designed artificial nest experiments may provide an independent source of data (i.e., a measure of potential predation pressure) that help explain how avian species may be adjusting to different predation pressures (Sieving and Willson 1998).

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